The North Atlantic subpolar gyre regulates the spawning distribution of blue whiting (Micromesistius poutassou Risso)

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The North Atlantic subpolar gyre regulates the spawning distribution of blue whiting (*Micromesistius poutassou* Risso)

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Abstract: The spawning stock of blue whiting, an economically important pelagic gadoid in the North Atlantic Ocean, increased threefold after 1995. The reproductive success of the stock is largely determined during the very early stages of life, but little is known about the spawning dynamics of this species. We here show that the spawning distribution of blue whiting is variable, regulated by the hydrography west of the British Isles. When the North Atlantic subpolar gyre is strong and spreads its cold and fresh water masses east over the Rockall Plateau, the spawning is constrained along the European continental slope and in a southerly position near the Porcupine Bank. When the gyre is weak and conditions are relatively saline and warm, the spawning distribution moves northwards along the slope and especially westwards covering the Rockall Plateau. The apparent link between the spawning distribution and the subpolar gyre is the first step towards understanding the reproduction variability, which currently is the main challenge for appropriate management of the blue whiting stock.

Keywords: Long-term, Climate variability, North Atlantic Subpolar gyre, Fisheries, Spawning distribution.

Introduction

The northern blue whiting (*Micromesistius Poutassou* Risso) is a pelagic gadoid mainly occupying the waters between the spawning grounds west of the British Isles and the feeding areas in the Norwegian Sea (Bailey 1982). The spawning stock of blue whiting has increased dramatically in the late 1990s (Fig. 1) due to a succession of strong or extremely strong year classes (ICES 2007). The fishery intensified correspondingly and has in recent years been one of the largest fisheries in the North Atlantic Ocean (ICES 2007). Concurrent large changes have occurred in the ocean circulation in the north-eastern Atlantic (Hakkinen and Rhines 2004), resulting in a rapid temperature and salinity increase west of the British Isles after the mid-1990s (Hatun et al. 2005; Figs. 1 and S1). Noting the tight temporal correlation between these events, we here ask whether the changes in marine environment and the blue whiting stock are causally related.

Possible causal relations are probably complex as the environment influences many ecological components simultaneously. Blue whiting are sensitive to temperatures and salinities during the spawning period (Schmidt 1909), and the main spawning grounds are located west of the British Isles (Fig. 2), where large oceanographic changes are known to take place (Holliday 2003).

The water-masses of the north-eastern Atlantic at different depths have different origins with their own recognizable planktonic fauna or flora, according to their physical, chemical, biochemical or biological features (Fraser 1961). The subpolar gyre controls the flow trajectory of the North Atlantic Current (NAC) in the north-eastern Atlantic. When the gyre is strong and extends far eastwards, a branch of the NAC peels off into the Rockall Trough, dragging cold and low-salinity subarctic waters over the Rockall Plateau (Fig. 3a). When the gyre weakens and shifts westwards, it allows subtropical water to spread north and west (Fig. 3b), resulting in much

warmer and more saline conditions. The strength of the subpolar gyre, and thus the hydrographic conditions in the Rockall region, has been represented by a so-called *gyre index* (Hatun et al. 2005; Fig. S1)

Since blue whiting are sensitive to hydrography while spawning in a region characterized by large water mass exchanges, one might expect that the marine climate must influence the spawning distribution of blue whiting. The blue whiting fishery has historically been most intensive along the European continental slope, primarily near the Porcupine Bank, but also west of the Hebrides, as illustrated in Fig. 2. These areas are typically thought of as the main spawning grounds of blue whiting (Monstad 2004). However, investigations of blue whiting larvae before the fishery commenced in the late 1970s indicated, on the other hand, that the Rockall Plateau was the principal spawning ground, as opposed to the Porcupine Bank (Henderson 1957; Fig. 2). Thus, there are apparent conflicting statements about the spawning areas of blue whiting and only limited explanations for their spawning dynamics (Bartsch and Coombs 1997; Skogen et al. 1999).

The dominance of the Rockall Plateau as a spawning ground was particularly pronounced during the warm early 1960s, but the spawning distribution shifted southwards towards the Porcupine Bank during the late 1960s (Bainbridge and Cooper 1973) when temperatures decreased in the region (Fig. 1). The stark contrast between the spawning distributions reported during the mid-nineteenth century warm period and the cold early 1990s (Fig. 2) suggests a link between the marine environment and the spawning dynamics of blue whiting. Bainbridge and Cooper (1973) postulated that the source of this variable distribution probably involved environmental variables; that the source of this variability might be found in regions remote from the spawning areas and that they might affect the stock after a considerable time lag. They also

stated that further progress on this topic had to await better environmental data over a longer run of years.

Since that work was published, we have witnessed the large mid-1990 changes in both the recruitment (and stock size) of blue whiting and also in the marine climate. Additionally, physical time series are now available that link the previous (1960s) warm period to the recent (post-1995) warm period. It is therefore timely to look at the previous and the present spawning distributions and to collectively examine these in light of the oceanographic changes that have taken place.

In trying to approach the fundamental question of a causal link between marine climate and blue whiting reproduction, we here limit the aim to document a link between the spawning distribution of blue whiting and the variable marine environment in this region. The working hypothesis we explore here is that the spawning distribution is predominately controlled by the marine climate conditions to the west of Great Britain and Ireland, moving north along the European continental slope and west over the Rockall Plateau during (saline and warm) periods when the subpolar gyre is weak, and south towards the Porcupine Bank during (fresh and cold) periods when the gyre is strong.

Material and Methods

The NISE hydrographic database

A comprehensive hydrographic (temperature and salinity) dataset has been compiled in association with the project *Norwegian and Iceland Seas Experiment* (NISE). The basis of this dataset is the public database maintained by the International Council for the Exploration of the Seas (ICES) (www.ices.dk). This database is then supplemented by data from the Marine Research Institute, Iceland; Institute of Marine Research, Norway; the Faroese Fisheries

Laboratory; the Arctic and Antarctic Research Institute, Russia and Geophysical Institute, University of Bergen, Norway and the World Ocean Circulation Experiment (WOCE)(www.woce.org). The data used here (post-1980) are generally measured by CTD (Conductivity, Temperature, Depth) sondes, but data from the Argo float array (www.usgodae.org) have also been included. Data quality control has been performed by each data contributor, but some additional data cleaning has been applied to the dataset by NISE (Nilsen et al. 2008).

Acoustic biomass survey data

Acoustic abundance estimates of blue whiting in the spawning areas from 1981 and onwards were obtained from the annual blue whiting surveys reported in the ICES "Northern Pelagic and blue whiting Working Group" reports (ICES 2007) as biomass (tons) averages over 0.5° latitude x 1° longitude (1981-2001).

During the standardized surveys, continuous acoustic recordings of fish and plankton were collected along the cruise tracks using calibrated 38 kHz echo sounder systems. The acoustic recordings (area backscattering by each nautical mile, s_A) were allocated to blue whiting based on the composition of the trawl catches taken whenever needed to identify the acoustic scatterers as well as by visual scrutiny of the echo recordings, whereafter biomass estimates were calculated by multiplying abundance in numbers by the average weight of the fish in each statistical square (Foote 1987; Toresen et al. 1998).

The annual surveys were carried out from mid-March to mid-April with less than two weeks difference in timing. The error introduced by a variable timing in relation to the spawning progress should be minor compared to the large spatial shift revealed by these data. The surveys are widely regarded as representing the actual spawning distribution and not the pre or post-

spawning migrations. The most recent data (after 1995) originate from joint international surveys, while the older data are obtained predominately from Norwegian surveys, with two years from Russian surveys.

Furthermore, the fish present in the area at spawning time are mostly actively spawning blue whiting. The proportions of immature fish in the spawning area varied in most of the years between nil and 10%, with some exceptions, e.g. around 15% in 2001, 1998, and 1989, mainly due to rich year-classes contributing as young fish (1 or 2 group) in the area (ICES 2007). The survey coverage included the Porcupine Bank area, the shelf edge west of the Hebrides all years except in 1982, 1997 and 2001. The Rockall Plateau area has been regularly covered since 1998, but only occasionally during the 1980s and early 1990s (Fig. 4a).

Blue whiting larvae data

Blue whiting larvae data were obtained from the Continuous Plankton Recorder survey (CPR) (Reid et al. 2003). The survey is a monitoring programme using a high-speed plankton sampling machine that is towed at 10-m depths behind ships of opportunity on standard routes each month of the year. The data presented here are obtained from tows performed by Ocean Weather Ships patrolling the waters west of the British Isles from 1951 to 1970 (Bainbridge and Cooper 1973). These data have kindly been reworked and made available to us by Sir Alister Hardy Foundation for Ocean Science (www.sahfos.ac.uk).

Fisheries catch statistics

Under the NEAFC (North Eastern Atlantic Fisheries Commission, www.neafc.com) scheme, vessels report to their respective (national) Contracting Parties and this information is shared via the NEAFC Secretariat's database. The blue whiting catch statistics applied here are obtained

from this database. The data are available as monthly values of the total catch gridded onto 0.5º latitude x 1º longitude rectangles and differentiated for each national fleet. Data are exclusively used from the Norwegian fleet, as the spatial distribution of this fleet was not limited by political regulations. The other major fishing nations for blue whiting, the Faroe Islands and Russia had only limited or no access, respectively, to European Union waters during most of the period from 1980 to 2007. The fishery in spring is focused on spawning blue whiting. We assume that the figures given represent catches of adult spawning blue whiting with proportions of immature fish comparable to those in the surveys reported above, as the fishery tend to selectively concentrate on large (adult) and thus mature fish.

Regional gyre index

A regional gyre index, based on simulated sea surface height, has been produced here. This is done by repeating the analysis of Hatun et al. (2005), while limiting the analysis to a geographical region in the north-eastern Atlantic Ocean (54-66°N, 30-0°W). The regional index presented here is similar to the one presented by Hatun et al. (2005), except from a dip in the mid-1980s, which is largely ascribed to dynamics in the Irminger and Labrador Seas. The employed numerical Ocean General Circulation Model (OGCM) is the Nansen Center version (Bentsen et al. 2004; Drange et al. 2005) of the MICOM (Miami Isopycnal Coordinate Ocean Model) (Bleck et al. 1992), forced with daily mean NCEP/NCAR (Kalnay et al. 1996) reanalyses of fresh water, heat, and momentum fluxes for the period 1948-2003. Since this model system terminated in 2003, the gyre index has been extended to 2006 using satellite altimetry (Hakkinen and Rhines 2004, updated).

Use of spatial data transformations

The biological and physical data sets described above are generally scattered in both time and space, with variable resolution, making direct comparisons difficult. The survey biomass and the hydrographic data are most densely distributed along the European continental slope (roughly meridional) (Fig. 4), while the CPR larvae data are most densely distributed along track lines fanning out westwards from the continental slope towards Hatton Bank (Bainbridge and Cooper 1973). To enable meaningful comparisons, each dataset has been transformed onto a common axis, following the regions with densest data coverage.

To illustrate meridional shifts in the survey biomass and the hydrography along the European continental slope, these data have been transformed onto a curvilinear axis (*s*-axis) tracking the high density of observations along the continental shelf-edge, starting within the Porcupine Seabight in the south (50.5°N), and continuing with points along the slope north to 61°N, west of Shetland (Fig. 4). To illustrate blue whiting larvae distribution shifts on-off the Rockall plateau, the CPR larvae data are transformed onto a rectilinear axis (*r*-axis) extending from the continental slope north-westward towards the Hatton Bank (Fig. 8a).

The value at a given position *x* along these axes is calculated as a weighted average of the available observations within a truncation radius (r_0) around this position. If too few observations are available near a position *x*, the truncation leaves the transformed value void, instead of having it represented by only a few too remotely positioned observations. The transformed value at position *x* can be written as:

(1)
$$\hat{D}(x) = \frac{\sum_{i}^{N} D_i w(d_i)}{\sum_{i}^{N} w(d_i)}$$

where N is the number of observations (D_i) within the truncation radius r_0, and w is a weight, which is a function of the distance d_i from position x. A Gaussian weighting function was used, as it gives a smooth distribution and its properties are easily understood. This weight is given by:

$$w(d) = \exp\left(\frac{-d^2}{2\tau^2}\right) \quad (2)$$

where d is the distance between position x and the location of the observation, and τ is the width of the filter. Since we are interested in shifts in distributions more than the inter-annual abundance variations, the biological observations have been normalized by the annual along-axis mean.

Results

Meridional shifts

Survey biomass and the subpolar gyre

Meridional shifts in the concentration of spawning blue whiting along the European continental slope (s-axis) are seen to co-vary with the dynamics of the subpolar gyre (Fig. 5a). For transforming the survey data onto the s-axis, these biomass observations are regarded as data points located in the centre of each 0.5° latitude x 1° longitude square, as presented in the ICES reports. The Gaussian filter width (τ) and the truncation radius (r_0) were both 100 km, as this is comparable to the size of each data square. The denominator in equation (1) removes the effect of high or low survey coverage in an area, and the obtained value is thus consistent and comparable

along the entire *s*-axis. This gives a normalized Gaussian-weighted mean-density of blue whiting observed within a 200-km wide swath along the *s*-axis, including the spawning period every year since 1981 (Fig. 5a).

The regional gyre index is plotted onto the survey biomass map (black curve Fig. 5a), together with the salinity (red curve) observed along a section (Ellett Line; Fig. 4b) extending from the continental shelf towards the Rockall Bank across the northern Rockall Trough (Holliday et al. 2000). The salinity is averaged over depth range 0-800 m, and the time series illustrates the strong subpolar gyre related exchanges of water masses around Rockall, as previously demonstrated (Hatun et al. 2005). Salinity is shown since this is a more conservative tracer than temperature, and thus a better indicator for oceanic advection.

The gyre was relatively weak in the early 1980s, the salinities were high and whilst survey coverage is incomplete during this time, the available observations suggest that spawning has a northerly orientation, taking place on the shelf edge west of the Hebrides (~58°N) (Fig. 5a). The gyre intensified appreciably in the early 1990s, resulting in very low salinities and the largest spawning concentrations in the Porcupine Seabight, to the far south. The sudden weakening of the subpolar gyre after 1995 enforced a rapid increase in salinities and a clear northward shift of spawning activity. Since about 2003 the gyre has intensified slightly, salinities have again decreased and the spawning distribution has retracted somewhat toward the south. Statistical analysis shows significant correlations between the location of the maximum spawning concentrations on the *s*-axis and both the gyre index ($r = -0.56$, df =15, $p = 0.021$) and the average salinity on the Ellett Line ($r = 0.62$, df = 15, $p = 0.007$). Similar correlations are seen using the centre of mass of the distribution as the dependent variable instead of the location of the maximum.

Hydrographic threshold

The largest concentrations of spawning blue whiting are observed within specific salinity (Fig. 5b) and temperature (Fig. S2) ranges. Demonstrating this requires considerable hydrographic data distributed along the southward migration route of the pre-spawners. This data material is not available over the open ocean areas (Fig. 4b), and the analysis has therefore been done along the *s*-axis, bearing in mind that this might not entirely represent the environment experienced by the migrating fish.

The hydrographic data from the spawning period (March to June) were first interpolated onto 300-m depths using the software Ocean Data View (Schlitzer 2007). The salinity at 300 m, considered as representative of the environment experienced by spawning blue whiting (Bailey 1982), was then transformed onto the *s*-axis. The result was, however, not sensitive to the choice of depth, since the water column is rather homogeneous after winter convection. The Gaussian filter width (τ) and the truncation radius (r_0) were both 50 km (see Fig. 4b). This gives salinities at 300-m depths, along the continental slope from 50°N to 61°N, for the spawning period every year since 1981, as shown in the time-longitude (Hovmüller) plot in Fig. 5b.

The isohalines move south until 1995, followed by a subsequent northwards shift, resembling the variability of the subpolar gyre and the survey biomass (Fig. 5a). This shift is clearest for the 35.35 to 35.45 psu isohalines (black curves in Fig. 5b). A second point to note is that the anomalies occur in pulses – one around 1990, one around 1997 and one around 2003. The two latter pulses have their counterpart in the gyre dynamics, while the pulse around 1990 does not.

A similar analysis has been performed using temperatures (Fig. S2), leading to similar conclusions: Blue whiting prefers to spawn within relatively narrow ranges of salinity (35.35-

35.45 psu) and temperature (9-10°C), in gross agreement with previous findings (Henderson 1957; Schmidt 1909).

On-off the Rockall Plateau

Hydrography

The above analysis suggests that a salinity range of 35.35-35.45 psu, a temperature range of 9-10°C, or similar water mass characteristics related to these hydrographic ranges, govern the spawning distribution of blue whiting. If this result is generally valid, we would expect to see evidence of spawning activity throughout these water bodies, not just within the relatively narrow range covered by the ICES acoustic surveys considered here (Fig. 4a).

The mid-1990s weakening of the subpolar gyre (Hakkinen and Rhines 2004) (Fig. 5a) represents, as mentioned, a particularly pronounced shift from a subarctic influenced regime to a subtropical influenced regime. This period is thus used to depict the variable dynamics of the system. Composite maps of salinities at 300 m for the low-saline pre-1995 decade (Fig. 6a) and the saline post-1995 decade (Fig. 6b) illustrate that the salinity changes are even larger around the Rockall Plateau than near the continental shelf. The salinity interval (35.35-35.45 psu) in which most spawning is observed near the continental slope (Fig. 5b), does not cover the Rockall Plateau before 1995 (Fig. 6a), but does during the decade thereafter (Fig. 6b). A similar statement can be made based on temperatures (Fig. S3). Does this mean that blue whiting also spawned near the bank after 1995?

Fisheries

The distribution of the spawning-fishery provides some insight into this question. A marked westward shift occurred in the fishing location of the Norwegian fleet during the mid-1990s (Fig. 7). No catches of blue whiting are reported west or south-west of the Rockall Bank before 1996 (Fig. 7a), while very large catches are reported there after 1996 (Fig. 7b). The Norwegian fleet was not greatly-limited by political regulations in the Rockall region, and should therefore be a reasonably unbiased proxy for the distribution of spawning fish in this region. In the absence of more reliable biological observations of blue whiting, this data is an indication of significant spawning west of the Rockall Plateau after the 1995 hydrographic shift.

Rockall-continental slope larvae distribution and sea surface temperature (SST)

Historical observations of larvae from the CPR survey also provide insight into the presence of spawning over the Rockall Plateau. CPR larvae data from the northern Rockall Trough during the period 1951-1970 have been transformed onto a linear axis (*r*-axis) from the continental slope at 57°N extending north-westwards towards the Hatton Bank (Fig. 8a), using the Gaussian transformation scheme described above (eqs. 1 and 2). The Gaussian filter width (τ) and the truncation (r_0) radius were both 100 km (see Fig. 8a), in order to encompass a sufficient number of tows without spanning too wide. Only data from the spawning period March-June have been used. Currents in this region generally flow northwards parallel to the continental shelf (Fig. 3) (Ellett et al. 1986) and thus perpendicular to the *r*-axis, so that drift between spawning and the observation of larvae is not expected to greatly alter the east-west distribution. The analyzed data shows a clear east-west meandering of the larvae concentration evident in the longitude-time (Hovmüller) plot in Fig. 8b.

Data regarding salinity in this region are sparse during this early period, and we are forced instead to use SST as a proxy of oceanographic conditions. Comparison with the simulated gyre index in recent times shows that SST represents to first order the oceanographic changes in the region (Fig. S1). However, due to the spin-up period of the numerical ocean model (whose integration started in 1948), the SST time series is considered to be a more reliable measure of oceanographic conditions for the early 1950s-1960s period.

When the SST time series is plotted onto the larvae map (red curve in Fig. 8b), good qualitative agreement is seen between the east-west distribution of the larvae and the average SST in this region. Warmer temperatures are seen to cause a westward shift in the larval distribution towards the Rockall Plateau. Statistical analysis shows a significant correlation between the location of the maximum larvae concentrations on the *r*-axis and the SST (r = -0.50, df = 18, p = 0.024). A similar correlation is seen using the centre of mass of the distribution as the dependent variable.

Discussion

Blue whiting distributions during a century

We here show that the spawning distribution of blue whiting is determined by the oceanographic conditions to the west of Great Britain and Ireland, which in turn are regulated by the North Atlantic subpolar gyre. A century after Schmidt (1909) made the first mapping of the blue whiting distribution, we have now begun to understand how climate and large-scale oceanography shifts and warps this distribution. The first mapping was made during the coldest years (1904-1908) of the twentieth century and Schmidt (1909) observed a “striking absence” of fry west of the Rockall Bank, while significant amounts of fry were observed near the Porcupine

Bank. The distribution of fry observed with the CPR during the rapidly warming period from 1948 to 1955 contrasted with Schmidt's findings, as no fry were observed near the Porcupine Bank, while large concentrations were observed around the Rockall Plateau (Henderson 1957). The larvae concentrations decreased in the north and increased further south during the late 1960s, when the climate again deteriorated and temperatures declined (Bainbridge and Cooper 1973).

Using acoustic survey data along the continental slope, we have shown that spawning fish were aggregating at a northerly position during the early 1980s, but shifted again southwards towards the Porcupine Bank during the late 1980s and especially during the very fresh and cold early 1990s. After the dramatic decline of the subpolar gyre in 1995, the fish concentrations shifted about 1400 km northwards along the continental slope. The spawning distributions of blue whiting reported here and in the literature, can therefore be better understood by putting them in a century-long hydro-climatic perspective. These hydro-climatic changes have been attributed to the subpolar gyre dynamics for the post-1960 period (Hatun et al. 2005), but the gyre forcing might also have been dominating during the pre-1960 period, although data are too scarce to show this.

On-off Rockall

In this study, we especially want to draw attention to rapid changes in the spawning distribution to include the Rockall Plateau. Coverage by the acoustic surveys is inconsistent in this area, and no larvae data are available to document a possible sudden increase in spawning near Rockall after 1995. The fishery catch statistics, however, do indicate a marked shift after 1995.

Re-analyzing the blue whiting data presented by Bainbridge and Cooper (1973), while focusing on the Rockall Plateau-continental slope dimension, we showed marked on-off Rockall shifts during the two decades 1951-1970. Comparing this with the sea surface temperatures (SST) in the region revealed consistent near-Rockall distributions during warm years, and a near-slope distribution during colder years. This result is consistent with our hypothesis of intensive spawning near Rockall during the warm post-1995 period. The apparent conflicting depictions of the spawning distribution of blue whiting presented by Henderson (1957) and Monstad (2004) can thus be explained by the fact that they represent warm and cold regimes, respectively.

Hydrographic escort

We have discussed the spawning dynamics in relation to temperature and salinity mostly because these parameters are widely available and facilitate a century-long perspective on the marine environment-blue whiting link. Henderson (1957) stated that a hypothesis of too high temperatures for spawning near the Porcupine Bank during the 1950s was hardly tenable considering that the same fish species also spawns in the much warmer Mediterranean Sea. In this regard, it is important to understand that SST and salinity changes in the north-eastern Atlantic are proxies for large water mass exchanges. Such redistribution of water masses not only alters temperatures and salinities, but also chemistry and plankton contents in the ocean. The indication that most spawning occurs within narrow ranges of salinities (35.35-35.45 psu) and temperatures (9-10°C) could therefore be an expression of pre-spawning fish seeking the chemical clues or the plankton composition contained by water masses with this temperature-salinity signature.

The spawning distribution must, irrespective of the actual guidance mechanism, be determined during the late winter period when the fish is migrating southward. An instructive example of

how this may work is that of mackerel (*Scomber scombrus*), a pelagic species with spawning migration dynamics that resemble that of blue whiting. For this species it has been demonstrated that the southward migrating fish swim fast when they are in cold water, but slow down when they encounter warmer waters (Reid et al. 1997). This characteristic has been called *enviroregulation* (Neill 1984). An evolutionary process may have 'programmed' this fish species to deliver their eggs in a specific marine climate and fauna which maximizes the survival of their offspring. If enviroregulation also governs the southward migration of blue whiting, this can explain the association between hydrography and spawning distribution. For example, the preferred hydrographic range does not encompass the Rockall Plateau during the low-saline and cold pre-1995 decade, so pre-spawners located near the bank will continue to swim southeastwards along the salinity/temperature gradient, and thus towards the Porcupine Bank. Alternatively, during the post-1995 period the preferred hydrographic conditions cover the Rockall Plateau, so ripe fish first entering this region will not continue to swim southward, but rather start spawning.

A coherent picture from vague components

To illustrate both the long-term and the large-scale changes in the spawning distribution of blue whiting, it has been necessary to utilize many, widely-differing data sources. While each individual source does not provide conclusive evidence supporting our hypothesis, taken together, this material gives a consistent picture of the spawning dynamics.

The acoustic survey biomass is associated with uncertainties due to the acoustic method itself and the timing and spatial coverage of the cruises. Although individual years and details of the survey distribution might be unreliable, the characteristic southward shift until the mid-1990s, followed by a northward shift is probably a real signal.

The similar pattern seen in the meridional shifts of isohalines along the continental slope are also believable, although data from both near-shelf and more off-shore locations have been included. The data coverage is sparse until 1987, but relatively good thereafter as shown with the black crosses in Fig. 5b. The basic patterns discussed are not greatly influenced by data limitation after 1987. Aliasing due to the seasonal cycle is found to be insignificant since the seasonal salinity variability at 300 m is much smaller than the interannual variability. Only using data during late spring-early summer (March to June) further alleviates the aliasing problem.

The mid-1990 salinity changes at 300-m depths were illustrated by lumping scattered observations into a pre-1995 decade and a post-1995 decade, and applying an objective mapping technique (Bohme and Send 2005). Although this is a crude depiction, it probably illustrates the northward flush of high-salinity water in a realistic way, due to the large extent of the mid-1990s salinity changes. We also feel that the extent of the mid-1990s changes in the fishery must be caused by a real shift in the spawning stock, despite the fact that fishery statistics often are strongly biased by mis-reporting, and that the number and efficiency of the trawlers increased greatly during the mid-1990s.

Some doubt has been cast on how well larvae data represent spawning distribution since the larvae can have drifted considerable distances since spawning (Bainbridge and Cooper 1973). Furthermore, the larvae data are sampled at 10-m depths and can be significantly influenced by aperture avoidance. The sampled routes towards the weather ships vary somewhat, and the approach of decomposing these data onto an axis (*r*-axis) could therefore be questioned (Henderson 1957). But the close co-variability between SST and the east-west meandering of the larvae distribution still lends credibility to the result. However, the very low larvae counts near the continental slope during warm years do probably not reflect an absence of spawning there. It

more likely reflects a northerly spawning distribution and that the eggs may have been either spawned to the north of the *r*-axis, or already drifted north prior to the time of sampling.

Outlook and recruitment

Our ability to link the spawning distribution of blue whiting to the dynamics of the subpolar gyre is perhaps the most promising result in this study. Using realistic numerical ocean models, oceanographic databases and satellite-based observations (Hakkinen and Rhines 2004; Hatun et al. 2005), it is now possible to better understand the dynamics of this gyre and its atmospheric forcing mechanisms (Eden and Willebrand 2001). These issues are not further elaborated here, but will constitute the basis for future work aiming at a better understanding of the blue whiting stock dynamics.

Having established a link between the spawning distribution and the marine climate, the next challenges are to explain how the changeable spawning distribution might influence the recruitment to the blue whiting stock. The large shifts in the marine environment will probably influence larvae growth conditions both near the continental slope and near the Rockall Plateau. Assuming that the on-off Rockall Plateau variability of blue whiting spawning activity is the most important mechanism underlying the pronounced recruitment variability, we suggest the following causal relations. Firstly, that eggs and fry starting on the plateau will follow different drift paths from those starting on the shelf, which would enlarge and diversify their nursery area and thereby improve growth/survival opportunities of the larvae. Secondly, that a potentially strong retention of water masses near the Rockall Bank during warm low-gyre index years (Dooley 1984) might provide good local growth conditions. Thirdly, that larval development near Rockall might be in closer synchrony with production cycles of key prey types (zooplankton), than nearer the continental slope (Bainbridge and Cooper 1973).

Differentiating between these competing hypotheses is a challenging task which should be validated by i) applying hydrographic drift modeling to investigate how the initial position of eggs and larvae might influence the downstream spread of larvae and the environment they encounter, ii) establishing regular field studies to sample larvae growth/size and feeding intensity/food content simultaneously in the spawning areas and in the downstream larval feeding areas, and relate this to the ambient prey availability and the hydrographic environment and iii) examining expected east-west shifts in the distribution of 0 and 1-year-old blue whiting, by using annual demersal trawl surveys on the Icelandic, Faroese, and North Sea Plateaus (cf. Heino et al. 2008).

Such questions must be understood before reasonable predictions of the dynamics of the blue whiting stock in a changing environment, natural or man-made, can be made.

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Figure captions

Fig. 1. Changes in the sea surface temperature (SST) in the north-eastern Atlantic (thin line) and in the spawning stock biomass (SSB) of blue whiting (thick line). The annually averaged SST time series is obtained from the Hadley Centre SST data set (HadSST2) (Rayner et al. 2006), by averaging over a geographical box covering the north-eastern Atlantic (52.5-62.5°N, 27.5-12.5°W). The SSB time series (ICES 2007) has been shifted three years forward in time, which is the time required for new recruits to contribute to the stock biomass.

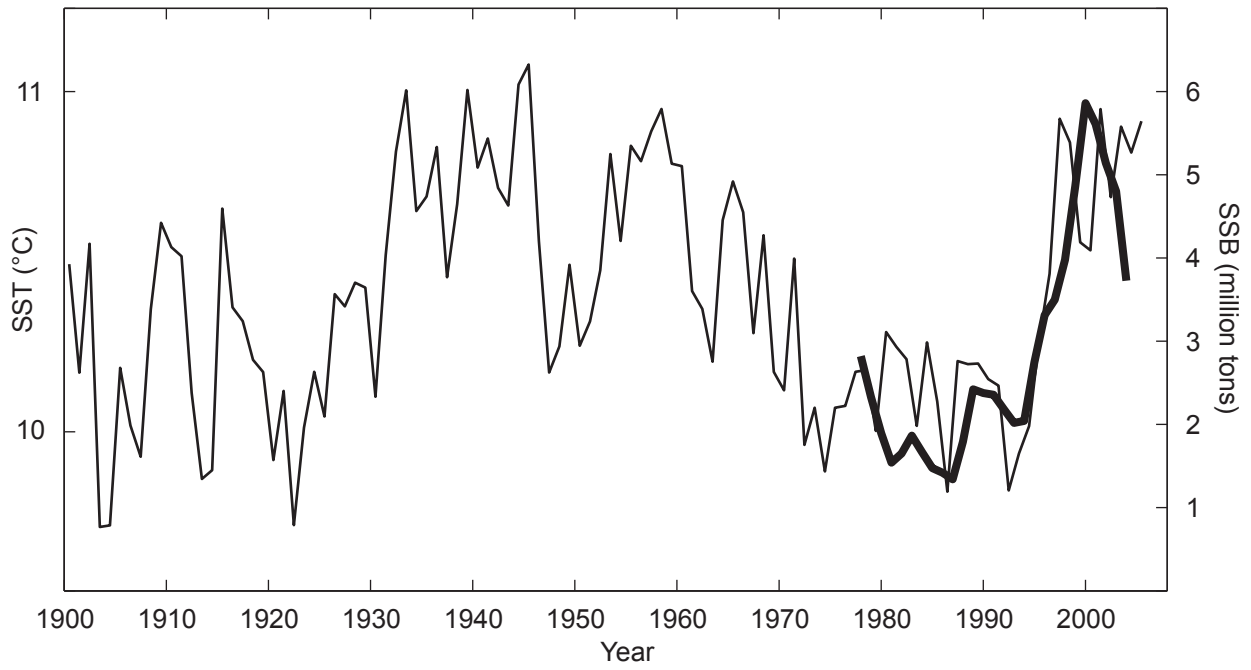
Fig. 2. Map of the study region, showing places referred to in the text. The gray contours show the mean density of blue whiting larvae during the years 1948-1956 as reported by Henderson (1961). No larvae data are available in the region west of the dashed line (southern part of the Rockall-Hatton Plateau). The intensive spawning areas during the 1980s and early 1990s, as reported by Monstad (2004), are shown in black along the European continental slope.

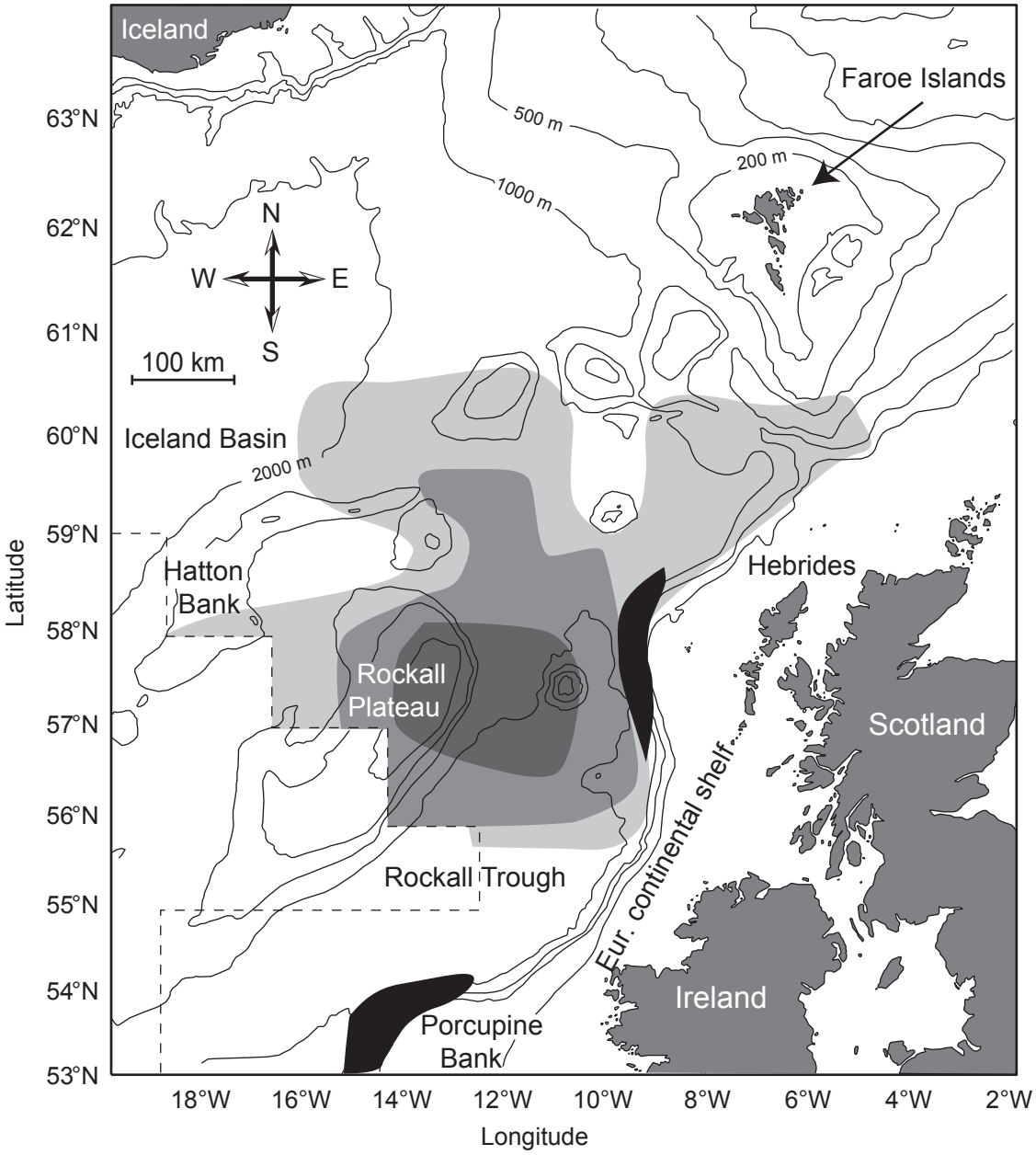
Fig. 3. Simplified illustration of the source flows to the Rockall Region. (*a*) A strong subpolar gyre results in strong influence of cold subarctic water near the Rockall Plateau (subarctic state). (*b*) A weak gyre results in a warm subtropical anomaly near the plateau (based on Hatun *et al.* 2005) (subtropical state). Abbreviations - RP: Rockall Plateau and PB: Porcupine Bank.

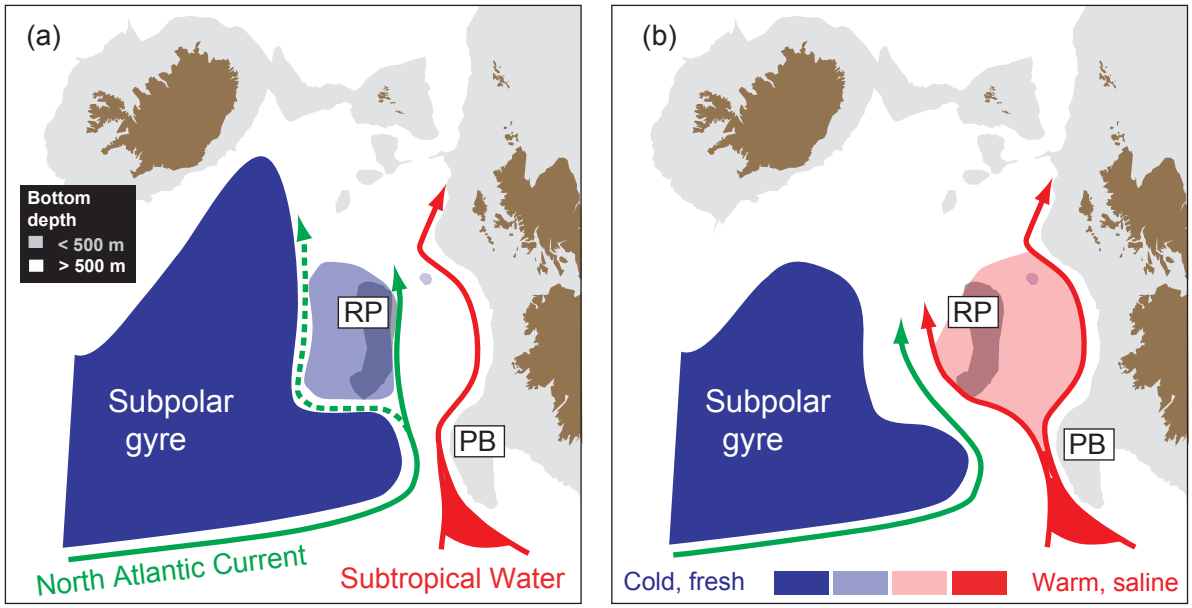
Fig. 4. Data coverage and the *s*-axis. (*a*) Spatial coverage of acoustic surveys (1981-2007) showing the fraction coverage of each 0.5° latitude x 0.5° longitude square and (*b*) number of hydrographic stations with available data at 300 meter depths during the 1981-2007 period, binned into the same geographical squares. Squares with no acoustical data or fewer than five

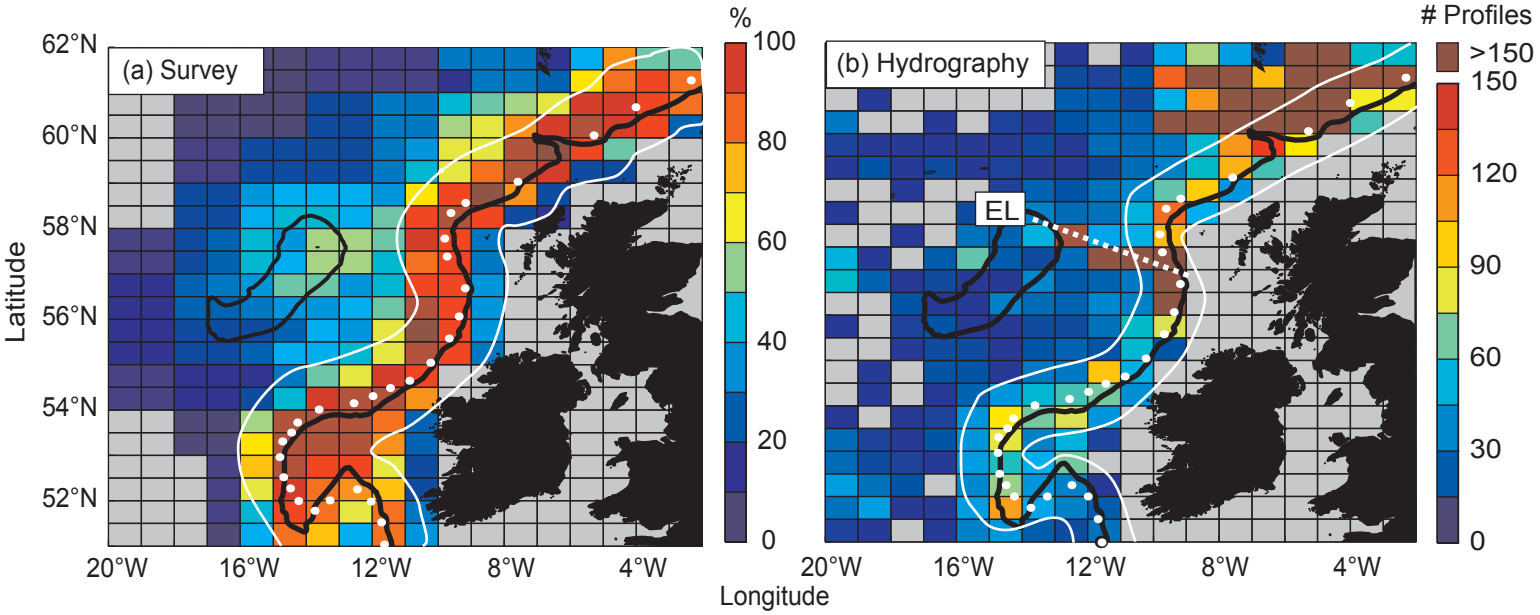
595 hydrographic stations are colored gray. The s-axis is shown with the dots and the truncation
596 radius (r_0) is illustrated with white thin lines. EL: Ellett Line.
597
598 **Fig. 5**. (*a*) Time-latitude/distance (Hovmüller) plot of normalized biomass density of blue
599 whiting along the European continental slope (*s*-axis, see Fig 4). The thick black curve shows a
600 gyre index based on the simulated sea surface height in the north-eastern Atlantic, and the dashed
601 black line shows an extension of this index based on satellite altimetry (Hakkinen and Rhines
602 2004, updated). The red curve shows salinity averaged over depth range 0-800 m at the Ellett
603 Line (Holliday et al. 2000) (see Fig 4b). White areas indicate absence of survey data. (*b*)
604 Hovmüller plot of salinity at 300-m depths along the *s*-axis. Only data from March to June have
605 been included. The salinity range (35.35-35.45) encompassing the densest blue whiting
606 observations in (*a*) is emphasized with thick black lines. Available data points are illustrated with
607 small crosses.
608
609 **Fig. 6.** March-June temperature composites at 300-m depths for (*a*) the fresh pre-1995 years
610 (1986-1995) and (*b*) the saline post-1995 years (1996-2005). The 35.35 and 35.45 isohalines (see
611 Fig. 5b) have been emphasized with thick black dashed lines. RP: Rockall Plateau.
612
613 **Fig. 7.** Distribution of adult catches of blue whiting reported by the Norwegian fleet, averaged
614 over (*a*) the low-saline and cold years from 1989 to 1996 and (*b*) the saline and warmer years
615 from 1997 to 2005. The area of each dot is proportional to the amount of blue whiting fished
616 within a 0.5º latitude x 1º longitude rectangle centered on the dot.
617

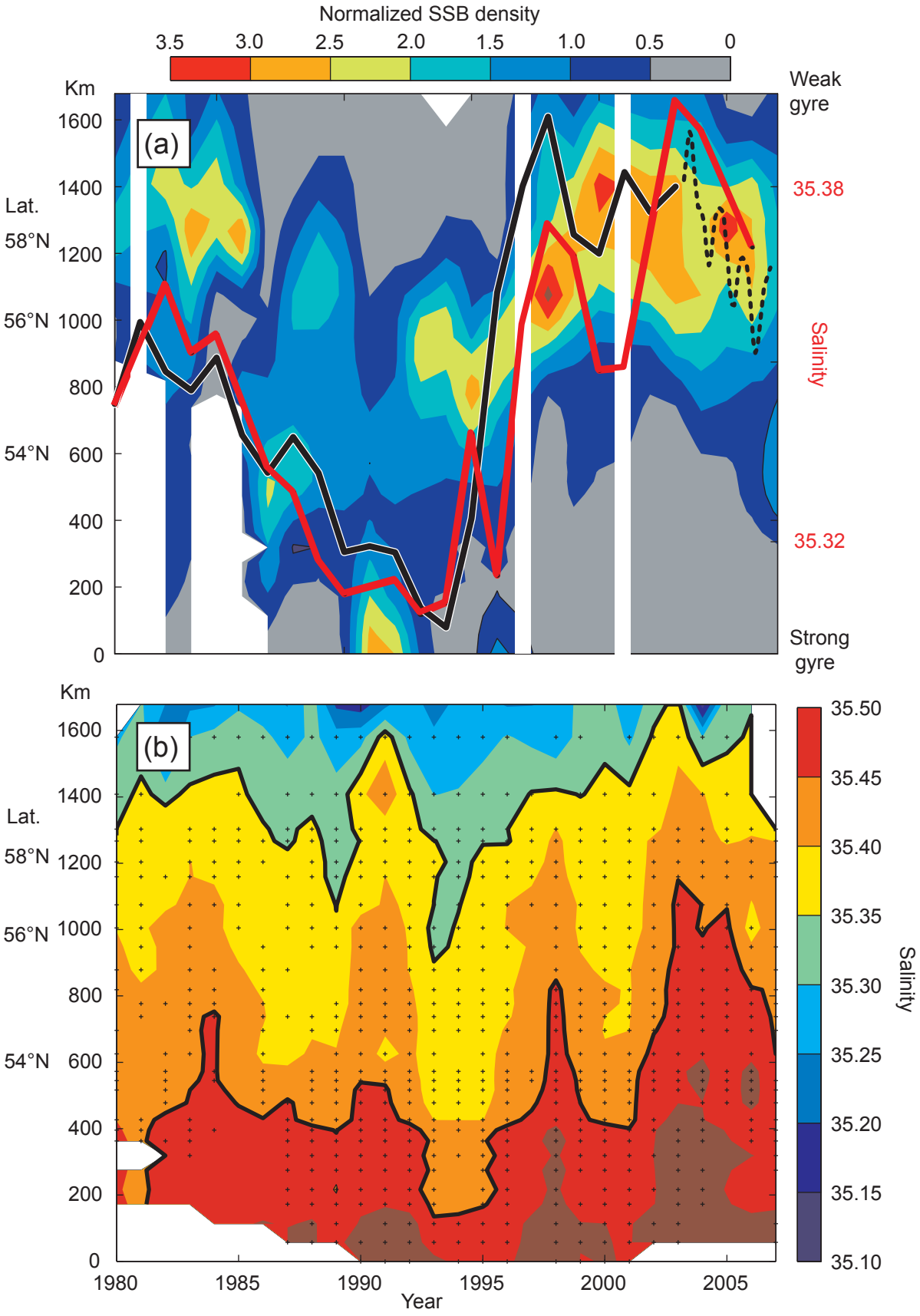
Fig. 8. (*a*) The *r*-axis (black dots) and positions with larvae data from the CPR (red dots) during the period from 1951 to 1970. The truncation radius (r_0) is shown with the blue dashed lines. (*b*) Longitude-time (Hovmüller) plot of the normalized larvae counts. The red line shows the sea surface temperature (SST) as described in Fig. 1. Available data points are shown with the crosses.

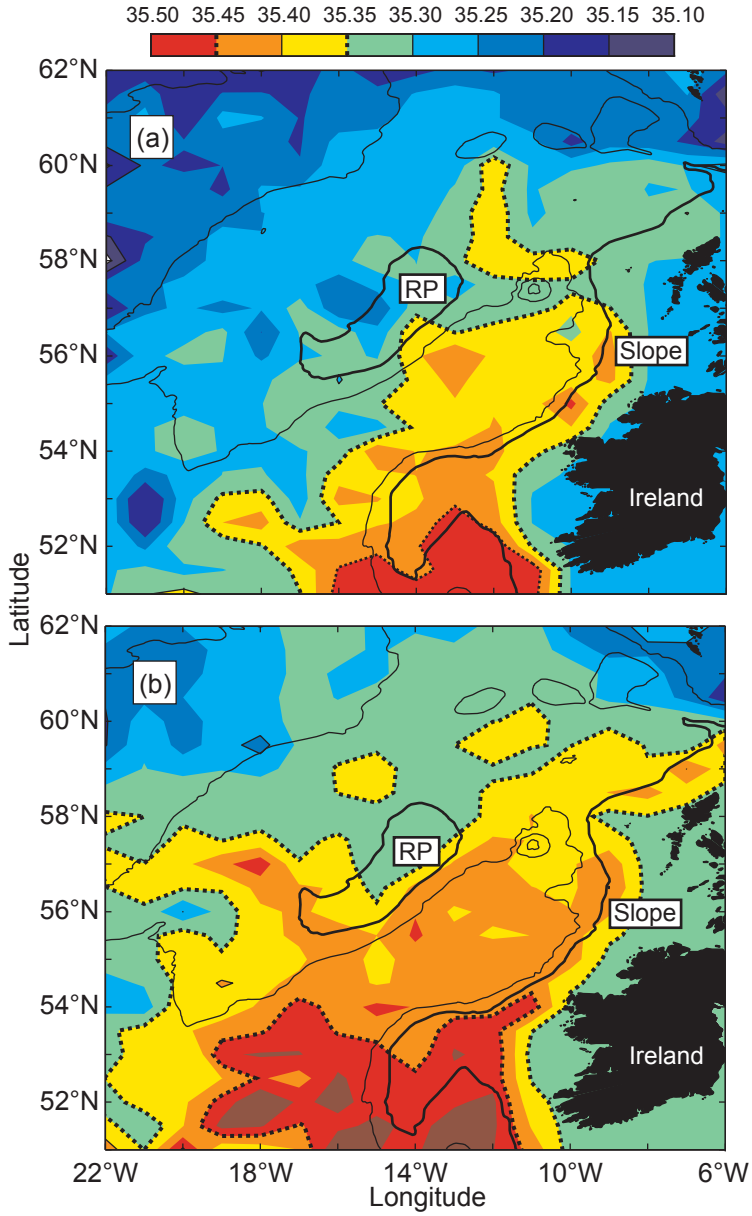


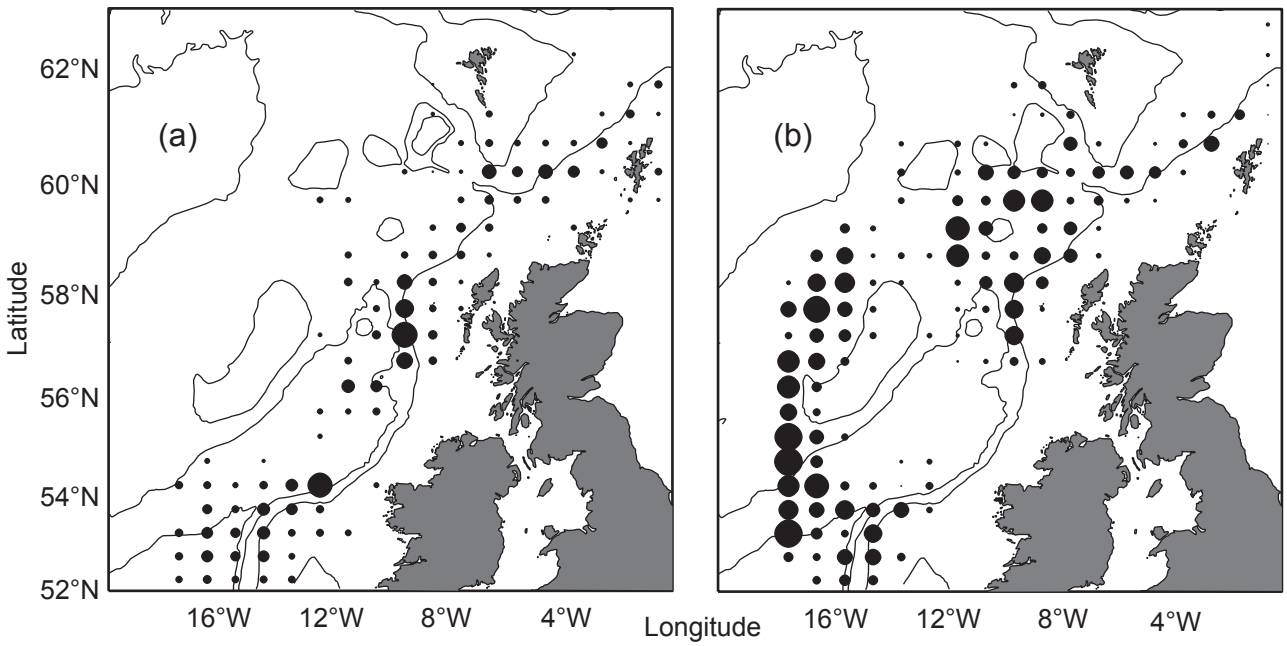

Iceland
Faroe Islands
500 m
200 m
1000 m
N
W
E
S
100 km
Iceland Basin
2000 m
Hatton
Bank
Rockall
Plateau
Rockall Trough
Hebrides
Scotland
Eur. continental shelf
Ireland
Porcupine
Bank
63°N
62°N
61°N
60°N
59°N
58°N
57°N
56°N
55°N
54°N
53°N
Latitude
18°W
16°W
14°W
12°W
10°W
8°W
6°W
4°W
2°W
Longitude

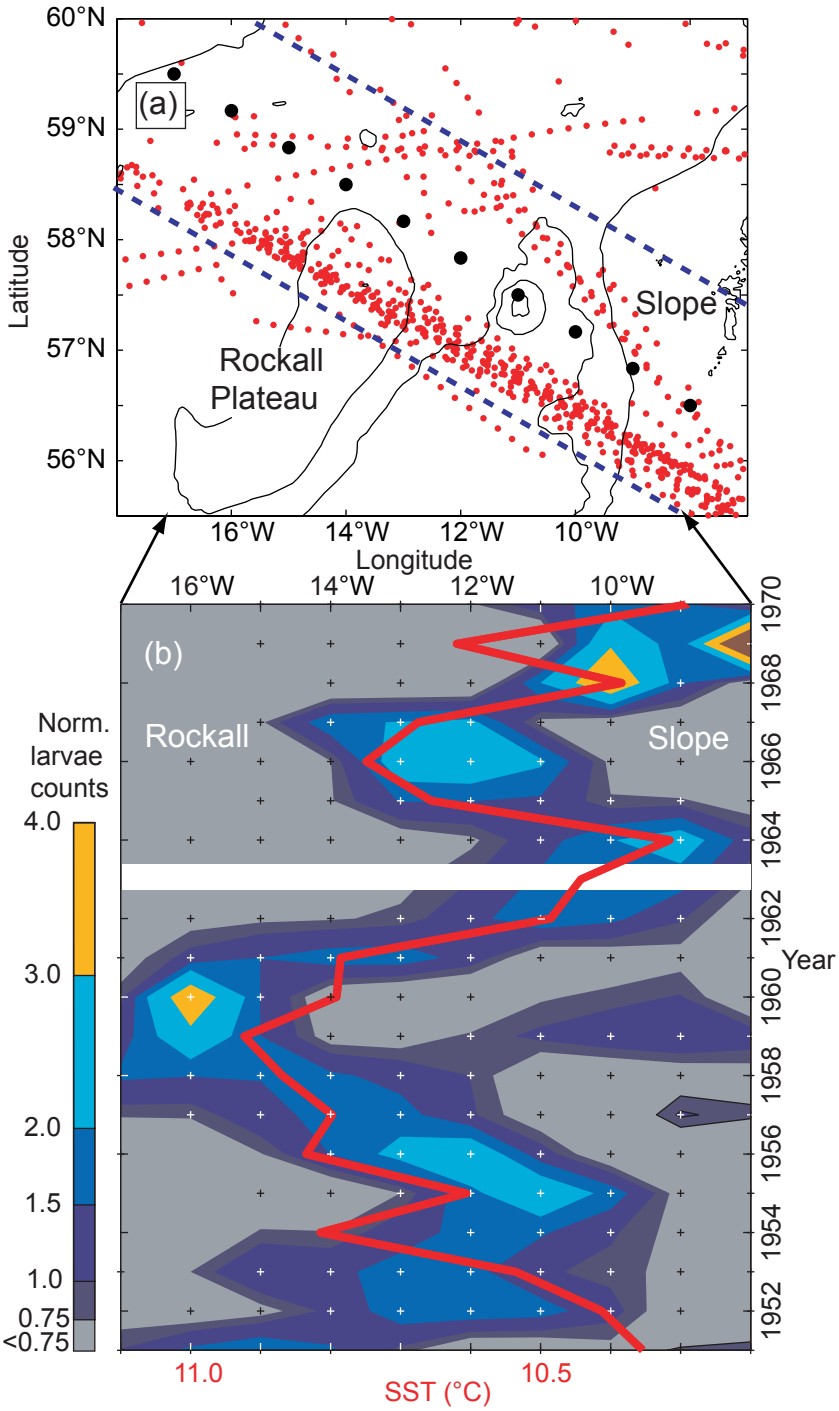

(a)
Bottom depth
< 500 m
> 500 m
RP
Subpolar gyre
PB
North Atlantic Current
Subtropical Water
(b)
RP
Subpolar gyre
PB
Cold, fresh
Warm, saline


(a) Survey
(b) Hydrography
EL
%
100
80
60
40
20
0
Profiles
>150
150
120
90
60
30
0
62°N
60°N
58°N
56°N
54°N
52°N
Latitude
20°W
16°W
12°W
8°W
4°W
Longitude


Normalized SSB density
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
Km
1600
1400
1200
1000
800
600
400
200
0
(a)
Lat.
58°N
56°N
54°N
Weak gyre
35.38
Salinity
35.32
Strong gyre
Km
(b)
Lat.
58°N
56°N
54°N
35.50
35.45
35.40
35.35
35.30
35.25
35.20
35.15
35.10
Salinity
1980
1985
1990
1995
2000
2005
Year


35.50 35.45 35.40 35.35 35.30 35.25 35.20 35.15 35.10
(a)
(b)
RP
Slope
Ireland
62°N
60°N
58°N
56°N
54°N
52°N
Latitude
22°W
18°W
14°W
10°W
6°W
Longitude


(a)
(b)
62°N
60°N
58°N
56°N
54°N
52°N
Latitude
16°W
12°W
8°W
4°W
Longitude


60°N
59°N
58°N
57°N
56°N
Latitude
(a)
Rockall
Plateau
Slope
16°W
14°W
12°W
10°W
Longitude
(b)
Rockall
Slope
Norm.
larvae
counts
4.0
3.0
2.0
1.5
1.0
0.75
<0.75
1952
1954
1956
1958
1960
1962
1964
1966
1968
1970
Year
11.0
10.5
SST (°C)